TAXONOMY OF *TETRAGONOTHECA* (ASTERACEAE-HELIANTHEAE)

B. L. TURNER and DEBORAH DAWSON

The University of Texas, Dept. of Botany, Austin, TX 78712

Tetragonotheca was first proposed by Linnaeus in 1753 to accommodate a single epappose species, *T. helianthoides*, which had been collected in the Carolinas by Gronovius. The genus receives its name from the four large, valvate, outer involucral bracts which house the florets and their associated receptacular scales or palea.

Gray, in 1841, described the second known species, *Tetragonotheca ludoviciana*. Because it had somewhat different, epappose, achenes he originally placed this in a newly erected genus, *Halea*. This was subsequently transferred to *Tetragonotheca*.

Engelmann and Gray, in 1848, added a third species, *Tetragonotheca texana*. Buckley, in 1861, added the fourth species, *T. repanda*, although Gray subsequently reduced this to varietal status under *T. ludoviciana*. The present treatment accepts the specific status of *T. repanda* and notes its relationship to be with *T. texana* instead of *T. ludoviciana*. In short, we recognize four allopatric species for the genus. So far as known, they do not intergrade or hybridize in nature.

Chromosome counts

Turner (1959) was the first to report chromosome numbers of *Tetragonotheca*, finding $n = 17$ pairs in three of the species examined. Shortly thereafter he counted the fourth species (*T. helianthoides*, $n = 17$). Voucher for the plants concerned are listed in Table 1. All counts were made from meiotic material at late diakinesis. At this stage bivalents show, characteristically, two chiasmata (Fig. 1). Subsequent workers (Table 1) have also found these several taxa to be diploid with $n = 17$ pairs.

Generic relationships

Most workers have placed *Tetragonotheca* in the tribe Heliantheae. Subtribal disposition has been somewhat more controversial. Both Bentham (1873) and Gray (1886) include it in the subtribe Verbesininae, as did Hoffmann (1893). Stuessy (1977), however, placed the genus in the subtribe Helianthinae.

Species from genera of yet other tribes have been inadvertently (or ignorantly) placed in *Tetragonotheca* (cf., excluded species), the most notable being *Guizotia abyssinica* (Coreopsideae) and *Rumfordia* (Melam-

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podineae). By inference, then, some relationship to these taxa may be postulated. It should be noted, however, that both *Guizotia* (Baagøe, 1974) and *Rumfordia* (Sanders, 1978) are but dubiously positioned in these tribes, having strong relationships with the Heliantheae.

It is our feeling that *Tetragonotheca* is relatively remote from any extant genus. Were it to have unspecialized, multiseriated involucral bracts, it would probably be positioned in the subtribe Helianthinae, near *Viguiera.*

ACKNOWLEDGEMENTS

In preparing distribution maps we have compiled records from those herbaria listed below (abbreviations according to Lanjouw and Stafleu, Index Herbariorum, Regnum Vegetabile 31: 1964). We are grateful to the institutes concerned for the loan of this material: the number of sheets borrowed, upon which the distributional maps are based, is shown in parenthesis.

ALA (5)	MO (94)*
DUKE (15)*	NC (62)*
FM (90)*	NY (92)*
FSU (29)*	SMU (82)
GH (100)*	TENN (41)
LAF (4)	TEX (100)
LL (50)	UC (29)*
MICH (27)*	US (122)*

This paper was originally begun in the early sixties by Mr. William L. McCart, graduate student at the University of Texas, Austin. Annotation of material from the above institutions marked with an asterisk (*) was undertaken at that time. Subsequent annotations have been made by the present authors.

Table 1. Chromosome counts in *Tetragonotheca.*

Species	Voucher* or reference	*n* number (pairs)
T. helianthoides	FLA. Alachua Co.: *Powell et al.* (1974)	17
	FLA. Columbia Co.: *Turner 4927.*	17
	FLA. Escambia Co.: *Turner 4919.*	17
	GA. Harris Co.: *Jones et al.* (1973)	17
	MISS. Lamar Co.: *Jones et al.* (1966)	17
T. ludoviciana	TEX. Montgomery Co.: *Turner* (1959)	17
T. repanda	TEX. Atascosa Co.: *Turner 4979.*	17
	TEX. Jim Hogg Co.: *Strother* (1972).	17
	TEX. Medina Co.: *Turner* (1959).	17
T texana	TEX. Travis Co.: *Turner* (1959).	17
	TEX. Travis Co.: *Urbatsch* (1974).	17

* On file, Plant Resources Center, Austin.

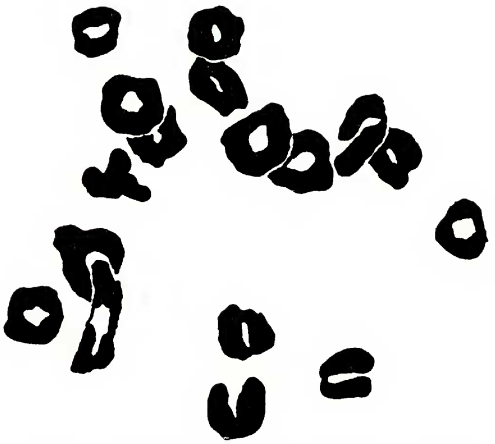

Fig. 1. Meiotic configuration at diakinesis in *Tetragonotheca helianthoides* (X 2600).

TETRAGONOTHECA L.

Tetragonotheca L., Sp. Pl. 2: 903. 1753.
Bikera Adans., Fam. 2: 130. 1763.
Gonotheca Raf., *in* Med. Repos. N. York 5: 352. 1808.
Halea T. & G., Fl. N. Amer. 2: 304. 1842.
Tetragonosperma Scheele, Linnaea 22: 166. 1849.

Coarse, erect, perennial, caulescent herbs with strong tap roots. Leaves opposite, simple, varying from nearly entire to coarsely-toothed to somewhat pinnatifid, their sessile bases often connate-perfoliate. Heads large, solitary, the disk and ray flowers yellow. Involucre double, the outer of 4 large, ovate phyllaries which are valvate in bud and remain united below forming a 4-angled or winged cup; the inner phyllaries membranous, as many as the ray flowers, and partly enclosing their achenes. Receptacles convex or conical, with narrow, membraneous chaff. Ray flowers pistillate, fertile. Disk flowers perfect, fertile. Style branches flattened, with marginal, stigmatic lines, the apices with an elongate hispid appendage. Achenes

quadrangular to sub-terete, truncate or rounded at the summit; pappus wanting or of several to numerous small, short scales. Basic chromosome number, $x = 17$ pairs. Type species: *Tetragonotheca helianthoides* L.

Key to species of *Tetragonotheca*

1. Pappus of 16 or more well-developed scales; plants of deep sandy soils in eastern and southern Texas.
   2. Leaves mostly basal, those on the main stem few, remote, and much reduced; peduncles stout, elongate, 5–40 cm long; plants of southern Texas ..... 3. *T. repanda*
   2. Leaves not mostly basal, those on the main stem well-developed, markedly perfoliate, the blades usually overlapping; peduncles 2–12(15) cm long; plants of eastern Texas ..... 2. *T. ludoviciana*
1. Pappus absent or a poorly developed fringe of ciliate scales (rarely comprised of 15 or fewer lacerate or fimbriate scales up to 1.0 mm long); plants of the south-eastern U.S. or of calcareous soils in south-central Texas and adjacent Mexico.
   3. Mid-stems leaves mostly 1–3(4) cm wide, markedly perfoliate-auriculate; involucral bracts mostly 8–15 mm long; plants of Texas and adjacent Mexico ..... 4. *T. texana*
   3. Mid-stem leaves (3)4–8 cm wide, not perfoliate; involucral bracts mostly 15 mm long or more; plants of the southeastern U.S. (east of the Mississippi River) ..... 1. *T. helianthoides*

1. TETRAGONOTHECA HELIANTHOIDES L. Sp. Pl. 2: 903. 1753. Type: VIRGINIA. *Gronovius 301.* Phototype (GH!)

Gonotheca helianthoides (L.) Raf., Med. Repos. N. York 5: 352. 1808.

Perennial herbs from stout tap roots. Stems commonly tufted, 3–10 cm tall, densely pubescent with crisp, spreading hairs (rarely glabrate or villous). Leaves broadly ovate to elliptical, sessile, mid-stem blades 5–20 cm long, 4–10 cm wide, acute or acuminate at the apex, remotely but sharply toothed or merely crenulate to nearly entire. Heads, excluding the rays, 2–4 cm across. Peduncles 5–8 cm long. Involucral bracts broadly ovate, 2–3 cm long, 1–2 cm wide. Ray florets 8–13, the ligules yellow, 2–4 cm long, 0.5–1.0 cm wide; tube 6–8 mm long, pubescent with spreading hairs. Disc florets greenish yellow; tube 1.5–2.0 mm long, sparsely to densely, crisp-spreading pubescent; throat 4–5 mm long. Achenes broadly clavate, turgid, subterete to somewhat 5(4)-sided, 4–6 mm long, striate, glabrous, epappose. Chromosome number, $n = 17$ II.

DISTRIBUTION AND ECOLOGY (Fig. 2). Mostly in sandy soils of cut-over pine and oak woodlands; southeastern United States, not known west of the Louisiana River. Flowering Apr–Aug.

Except for its vestiture, the species is remarkably uniform considering its wide distribution. On both morphological and chemical grounds (Urbatsch, pers. comm.), *T. helianthoides* seems closest to *T. ludoviciana*, ancestral populations from which it was presumably derived through regional isolation, loss of pappus and numerous other small but, in consort, significant diagnostic features.

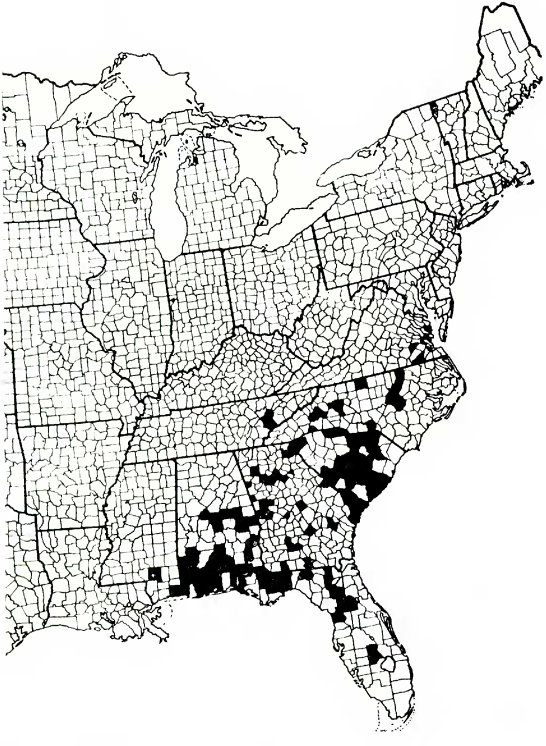

Fig. 2. Distribution, by county, of *Tetragonotheca helianthoides*.

2. TETRAGONOTHECA LUDOVICIANA (T. & G.) Gray ex Hall, Pl. Texanae 13. 1873.

Halea ludoviciana T. & G., Fl. N. Amer. 2: 304. 1841. Type: LOUISIANA. "Western Louisiana." Dr. *Leavenworth s.n.* (apparently collected before Jun 6, 1837, according to notation on the holotype). Holotype (NY!).

Perennial herbs from stout, elongate tap roots. Stems mostly single but sometimes tufted, especially following injury, densely white villous to glabrous. Leaves broadly triangular-ovate to somewhat repand, especially below, the mid-stem leaves nearly always connate or perfoliate, irregularly coarsely dentate to crenulate. Heads, excluding the rays, 1.5–3.5 cm across. Peduncles mostly short, slender, 2-8(12) cm long. Involucral bracts ovate, 1.0–1.8 cm long, 0.8–1.2 cm wide. Ray florets mostly 13, the ligules yellow, 1.0–1.8 cm long, 0.5–0.7 cm wide; tube 4–5 mm long, glabrous to sparsely pubescent. Disc florets yellow; tube ca 1.5 mm long, sparsely pubescent; throat 4–5 mm long. Achenes 4.5–6.0 cm long, 5(6)-sided, sparsely appressed pubescent; pappus a crown of 20–30 short, thickened, entire or erose, scales, 0.5–1.5 mm long. Chromosome number, $n = 17$ II.

DISTRIBUTION AND ECOLOGY (Fig. 3). Deep sandy, usually sterile, white soils of southeastern Texas and adjacent Louisiana. Flowering, Apr–Aug.

3. TETRAGONOTHECA TEXANA Gray & Engelm., Proc. Amer. Acad. 48. 1848. Type: TEXAS. Guadalupe Co.: Hills between the Guadalupe and Cibolo rivers, 12 mi W of New Braunfels, according to label data (MA), Apr 1846, *F. Lindheimer 431.* (Holotype, GH!; isotypes MO!, NY!, UC!, US!).

Halea texana (Gray & Engelm.) Gray, Proc. Amer. Acad. 83. 1849.
Tetragonosperma lyratifolium Scheele, Linnaea 22: 166. 1849. Type: TEXAS. Guadalupe Co.: Rocky soil, Cibolo River, Apr–May 1846? *Roemer s.n.* (Holotype, B).

Perennial herbs from tough tap roots. Stems mostly slender, solitary or tufted, only moderately branched above, 3–6(7) dm tall, frequently tinged with maroon, finely pubescent to glabrate. Leaves oblong, oval or elliptic in outline, pinnatifid, incised or repand, the lower-most merely connate, the upper connate-auriculate, 3–10 cm long, 2–4 cm wide. Heads, excluding the rays, 1–2 cm across. Peduncles elongate, slender, (8)10–25 cm long. Involucral bracts 1.0–1.5 cm long, 1.0–1.4 cm wide. Ray florets 8–13, the ligules yellow, 4–5(6) mm wide; tube ca 4 mm long. Disc florets yellow; tube ca 1 mm long, glabrous; throat ca 4 mm long. Achenes, obpyramidal, 3–4 mm long, pubescent, eppapose or sometimes with 4–12 small, ciliate scales. Chromosome number, $n = 17$ II.

DISTRIBUTION AND ECOLOGY (Fig. 3). Calcareous, rocky soils, or sometimes in mixed gravelly stream bottoms of south central Texas, extending into north central Mexico. Flowering Apr–Oct., depending on rains.

4. TETRAGONOTHECA REPANDA (Buckl.) Small, Fl. Southeastern U.S. p. 1250, 1340. 1903.

Helea repanda Buckl., Proc. Acad. Nat. Sci. Phila. 458. 1861. Type: TEXAS. Nueces Co.: "near Corpus Christi:" May w/o year, *Buckley s.n.* (Holotype, PH!). *Halea ludoviciana* var. *repanda* (Buckl.) Gray, Syn. Fl. N. Amer. 2: 256. 1884.

Perennial herbs from stout, elongate, tap roots. Stems 1–5 dm tall at first single but soon forming a short bushy habit through the production of stout laterals from the root-crown, minutely soft pubescent, particularly at the base and below the nodes. Leaves irregularly dentate, 3–12 cm wide,

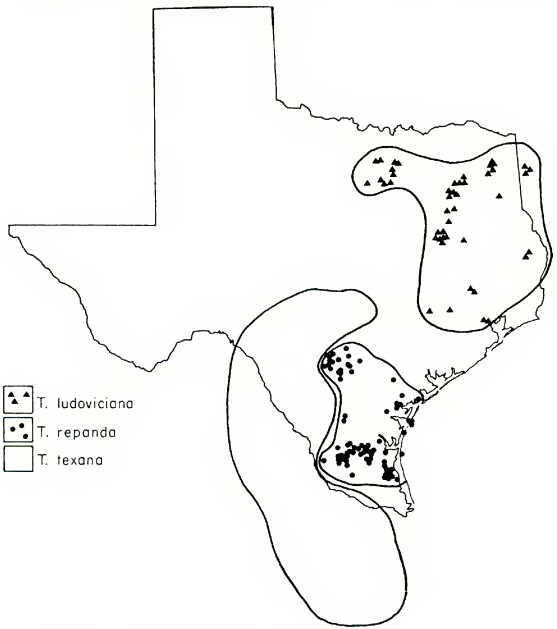

Fig. 3. Distribution of *Tetragonotheca* species.

12–24 cm long; blades of the rosette triangular with slender petioles; stem-leaves ovate, lanceolate to repand, narrowed into petiolar-like bases. Heads, excluding the rays, mostly 1.5–2.5 cm across. Peduncles stout, (5)10–40 cm long. Involucral bracts ovate to triangular-ovate, 1.1–2.0 cm long, 1.0–1.8 cm wide. Ray florets 16–24, golden-yellow, the ligules 2–3 cm long, 0.5–0.8 cm wide; tubes 5–6 mm long. Disc florets yellowish-green; tube glabrous to sparsely pubescent, 1–2 mm long; throat 4–5 mm long. Achenes 4.7–5.5 mm long, turgid, 4(5) sided, sparsely hispid-pubescent, especially along the angles; pappus a crown of 20–30 entire or erose scales, 0.3–1.5 mm long, those of the ray about 1/3 as long as those of the disc. Chromosome number, $n = 17$. II.

DISTRIBUTION AND ECOLOGY. (Fig. 3). Deep sandy soils of southern Texas and possibly adjacent Mexico. Flowering Mar–Nov., depending on rains.

Gray treated the species as a variety of *Tetragonotheca ludoviciana* but, as noted by Urbatsch *et al.* (1978; unpubl.), on chemical grounds it is closest to *T. texana*. It is also similar to the latter morphologically. In fact, occasional roseate or mowed plants of *T. texana* may be taken for *T. repanda*, but these can be readily identified by their epappose or fimbriate scales of the achenes, by their smaller leaves and generally slender stems.

Excluded Species

Tetragonotheca abyssinica Ledeb, Ind. Sem. Hort. Dorpat Suppl. 1824. = *Guizotia abyssinica* L. f. (Cf. Baagøe, 1974).

Tetragonotheca parviflora Jacq., Enum. Pl. Carib. p. 28, 1760 (from description and locality apparently not a *Tetragonotheca*).

Tetragonotheca guatemalensis Coulter, Bot. Gaz. 16: 99. 1891. = *Rumfordia guatemalensis* (Coult.) Blake, Wash. Acad. Sci. 18: 25. 1928 (Cf. Sanders, 1978).

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